

Nymph and egg of *Melanemerella brasiliانا* (Ephemeroptera: Ephemerelloidea: Melanemerellidae), with comments on its systematic position and the higher classification of Ephemerelloidea

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Abstract. The genus *Melanemerella* has been of uncertain familial placement since its description in 1920. It was first assigned to the family Ephemerellidae, later transferred to Tricorythidae, and finally to Leptohyphidae. The uncertain familial placement was partly a result of its unique characters and inadequate description based on a single female imago. We describe for the first time eggs and nymphs of both sexes. As a result of a cladistic analysis done to elucidate the correct family assignment of *Melanemerella*, we demonstrate that the genus is not a Leptohyphidae, Coryphoridae, or Tricorythidae. *Melanemerella* appears to be related to *Teloganella* (Teloganellidae) and *Manohyphella* (Teloganodidae), although the relationship is poorly supported. We propose the establishment of the family Melanemerellidae (new status) for this monobasic genus.

Key words: cladistics, systematics, taxonomy, neotropics, South America.

The discovery of a very unusual female imago of Ephemeroptera from Espirito Santo, Brazil, led Ulmer (1920) to establish the new genus *Melanemerella* for the new species *M. brasiliانا*. According to Ulmer (1920), this genus, although differing from the other genera of Ephemerellidae, showed some characters that clearly indicated it belonged to this family: the short intercalaries not joining the external margin, and the basal direction of the 3 anal and cubital veins of the forewings. Since then, the position of the genus has remained uncertain and much debate has been generated because it was known only from a female imago. A 2nd problem was that no other member of the family Ephemerellidae was ever recorded from South America, and including *Melanemerella* in Ephemerellidae thus posed a biogeographical problem.

In his extensive revision of the "Groupe Ephemerellidien", Lestage (1925) commented on the wing shape and venation of *Melanemerella*, concluding that it was a "specialized Ephemerellidae". Demoulin (1955), after analyzing the wing characteristics of Ephemerellidae and Tricorythidae (which included at that time the family Leptohyphidae), decided to transfer *Melanemerella* to Tricorythidae and established for it the subfamily Melanemerellinae. Edmunds et al. (1963) returned *Melanemerella* to Ephem-

erellidae, but retained the subfamily proposed by Demoulin.

Allen's (1965) revision of the family Ephemerellidae established the new subfamily Teloganodinae to include the genera *Teloganodes* Eaton, *Ephemerellina* Lestage, and *Teloganella* Ulmer, which were more related to each other than to *Ephemerella* Walsh, the only remaining genus in the subfamily Ephemerellinae. Although remarking that the relationship of *Melanemerella* would remain tentative until the male imago and nymphal stages were discovered, he stated that "The characters of the wings of *M. brasiliانا* suggest that it should be maintained as a separate subfamily in the Ephemerellidae". Lately, all authors followed Allen (1965) or Demoulin (1955) and considered *Melanemerella* to be an atypical Ephemerellidae or a primitive Tricorythidae, the sister group of Ephemerellidae (as constituted at that time).

Wang and McCafferty (1996) studied the adult female holotype of *M. brasiliانا* and concluded that there existed "critical evidence" to remove this genus from the Ephemerelloidea. This evidence included the shortness and untapered nature of the mesoscutellum and the full dorsal exposure of the methatorax, both considered plesiomorphies within Ephemeroptera. According to Wang and McCafferty (1996) the presence of gill socket remnants on the posterolateral extremities of abdominal segments 1 and 2 and the absence of polar caps in *Melanemerella*

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TABLE 1. Characters and character states.

		Character	
Life stage	No.	Description	States
Adult	0	Male compound eyes	0 = divided in upper and lower portions 1 = not divided
	1	Foretarsal claw of male imago	0 = similar (hooked) 1 = dissimilar 2 = similar (blunt)
	2	Apex of tibiae II and III ventrally extended	0 = absent 1 = small 2 = large
	3	Imaginal wing fringed with setae on hind margin	0 = absent 1 = present
	4	Base of vein CuA	0 = reaching R1 1 = detached from R1, directed to CuP
	5	Base of vein ICu1	0 = fused with or clearly directed to base of CuP 1 = free, or attached to CuA or CuP by cross veins 2 = fused with CuP at middle length (Tricorythid fork)
	6	Number of intercalary veins between CuA and CuP	0 = 3-4 1 = 2 2 = 0
	7	Detached marginal intercalaries	0 = present 1 = absent
	8	Attached marginal intercalaries	0 = present 1 = absent
	9	Hindwings	0 = present in both sexes 1 = present in male, absent in female 2 = absent in both sexes
	10	Length of costal projection/total length of hind wing	0 = very short (<0,2) 1 = medium length (>0,3 or ≤0,46) 2 = large (≥0,53)
	11	Location of costal projection	0 = from basal 1/3 to apex 1 = at the base
	12	Hindwings: number of longitudinal veins	0 = >5 1 = 3 2 = 2 3 = 1 4 = 0
	13	Forceps segments	0 = 2-segmented 1 = 3-segmented 2 = 4-segmented
14	Posterolateral corners of styliger plate posteriorly projected forming a columnar base for each forceps	0 = absent 1 = present	
Nymph	15	Fringed frontal shelf	0 = absent 1 = present
	16	Maxilla, number of setae on distal brush of galea	0 = <20 1 = >40
	17	Shape of prementum	0 = subequal or wider at apex 1 = wider at base
	18	Labial palp segments	0 = all subequal 1 = segment 3 reduced 2 = segments 2 and 3 reduced

TABLE 1. Continued.

Life stage	No.	Character	
		Description	States
	19	Form of femora	0 = elongated 1 = disc-like
	20	Transversal row of spines at base of femore II and III	0 = present 1 = absent
	21	Gills ventral lamellae	0 = bifid 1 = simple
	22	Branchial lobes	0 = absent 1 = only at base of lamellae 2 = along entire margin of lamellae
	23	Ventral lamellae, position of lobes	0 = bipinnate (dorsal and ventral) 1 = simple (ventral or lateral)
	24	Gill II, transverse weak band	0 = absent 1 = present
	25	Gill II	0 = normal 1 = opercular or semiopercular
	26	Abdominal gill I	0 = present, plate-like 1 = present, filamentous 2 = absent
	27	Abdominal gill 6	0 = present 1 = absent
	28	Abdominal dorsal tubercles	0 = absent 1 = single 2 = double
	29	Minute spines on posterior margin of abdominal terga III-V	0 = present 1 = absent
	30	Abdominal segments laterally expanded	0 = none 1 = 3-6 2 = 3-7 3 = 2 or 3-9
Egg	31	Number of polar caps	0 = 0 1 = 1 2 = 2

reinforced their decision to remove it from Ephemeroelloidea (both observations are in error, as discussed later). Wang and McCafferty (1996) decided to move *Melanemerella* to Leptophlebiidae, based on a series of characters that occur in various other families of Ephemeroptera, but with some doubts, stating "It is possible that *Melanemerella brasiliiana* is an unusual leptophlebiid. Moreover, it may be related to the also unusual leptophlebiid genus *Massartella*, or less plausibly, it may even be a species of *Massartella*". They concluded "... It is also possible that *Melanemerella* belongs to a new family of mayflies, but again the larva would be needed to establish such".

The Ephemeroelloidea is currently represented by 2 families in South America, the Leptohy-

phidae (composed of 8 genera with numerous species, and widely distributed), and its sister group, the Coryphoridae (monobasic, with a rather restricted distribution). *Melanemerella* is similar to *Coryphorus* in that both are known from only one species from very few, close localities.

We studied mayfly specimens of São Paulo State, Brazil, collected mainly by C. G. Froehlich (University of São Paulo) and his colleagues. Among the material were some nymphs that, based on developing wing venation, appeared to be the unknown nymphal stage of *Melanemerella*; no adults attributable to *Melanemerella* were found.

We describe the nymphal and egg stages of *Melanemerella* for the first time. Our intent is to

elucidate the relationships of *Melanemerella* based on a cladistic analysis that includes all the known South American genera of Ephemerelloidea, representatives of other members of this superfamily, and also *Massartella* (Leptophlebiidae), postulated by Wang and McCafferty (1996) as the probable genus where *Melanemerella brasiliensis* could be placed.

Methods

Preserved material

The nymphs used in this study were preserved in 80% ethanol. Wing pads were dissected from a full-size nymph that presented the wing membrane still unfolded, allowing observation of the veins. The wing pads were mounted on microscope slides with glycerin and drawn with a stereomicroscope camera lucida. The male genitalia from a mature nymph ready to moult were dissected and studied. Eggs were removed from a mature nymph, dehydrated in a graded ethanol series, and dried by the critical point method using CO₂ in a Bomar apparatus. Eggs were then mounted with double sided tape on SEM stubs and sputter coated with gold. They were observed and photographed with a JEOL 35CF scanning electron microscope at 25 kV.

Cladistic analysis

Taxa selection.—The objective of this analysis was to test the family placement of *Melanemerella*. Accordingly, we constructed a matrix with representatives of all the South American genera of Ephemerelloidea (8 Leptohyphidae genera plus *Coryphorus* and *Melanemerella*) and members of each of the families proposed for Ephemerelloidea by McCafferty and Wang (2000). As outgroups we used the genus *Neophemera* (Neophemeridae), a member of the superfamily Caenoidea (the supposed sister clade of Ephemerelloidea) and *Massartella* (Leptophlebiidae, Leptophlebiidae). We included *Massartella* in the analysis because it was postulated (Wang and McCafferty 1996) that *Melanemerella brasiliensis* could be a species of this genus, and we considered it necessary to test this hypothesis.

Characters and coding.—The characters and character states are listed in Table 1. The 32

characters included (16 from nymph, 15 from adult, and 1 from egg) were treated as binary (18 characters) or multistate (14 characters). The multistate characters 1, 6, 9, 10, 12, 22, and 31 were treated as additive because it was possible to hypothesize their sequence of change. The remaining multistate characters (2, 5, 13, 18, 26, 28, and 30) were treated as non-additive.

Analysis.—The matrix was analyzed with the computer program Parsimony with Implied Weights (PIWE) (P. A. Goloboff, 1993a. Parsimony with Implied Weights (PIWE) computer software, version 2.9, P. A. Goloboff, San Miguel de Tucumán, Tucumán, Argentina). PIWE is a program that resolves character conflict in favor of the characters that have less homoplasy on the trees. PIWE searches for trees with the maximum fit, which are the shortest trees (Goloboff 1993b). We prefer this particular weighting procedure (Implied Weights) because it takes into account additional information from the matrix (i.e., that homoplastic characters are less valuable for elucidating relationships).

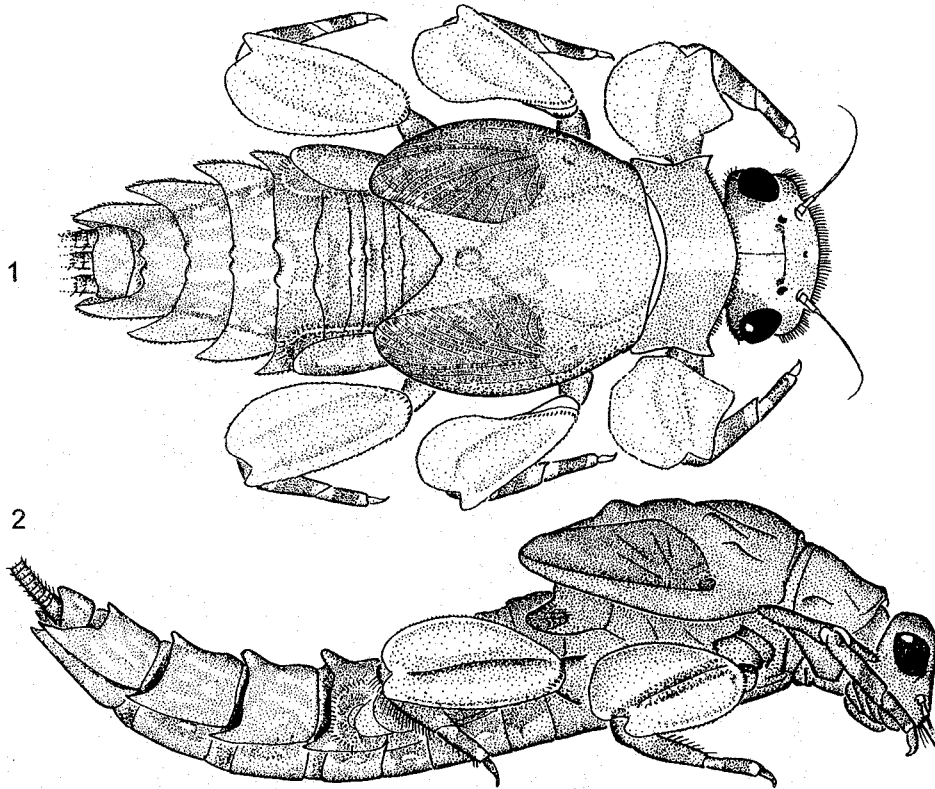
The search was done with the command "mult*" (with a set of 100 replications), which implements rearrangements of independently obtained Wagner trees using Tree Bisection and Reconnection (TBR). The default setting of the program for the weighting constant (K = 3) was used.

Neophemera and *Massartella* were independently used to root the tree, with no change in the position of *Melanemerella*. The computer program WinClada (K. C. Nixon, 1999. WinClada computer software, Bailey Hortorium, Ithaca, New York) was used to facilitate the diagnosis of characters, as well as drawing the trees. Bremer support (Bremer 1988, 1994) was calculated with the command "bs", using the tree of maximum fit and 799 trees up to 30.0 less fit (commands "hold 800" and "subopt 300", respectively).

Results

Family Melanemerellidae, new status Figs 1–35

Genera included: *Melanemerella* Ulmer.
Melanemerellinae (Tricorythidae) Demoulin 1955:214–216.
Melanemerellinae (Ephemerellidae) Edmunds et al. 1963:16.



FIGS 1, 2. *Melanemerella brasiliiana*, nymphal habitus: 1.—Dorsal view; 2.—Lateral view.

Nymph.—Eyes of male not divided. Fringed frontal shelf present. Labial palpi 3-segmented, distal segment reduced (Figs 14–16). Femora widely expanded (Figs 25–27). Hind wingpads present in both sexes. Gills present on abdominal segments 2–6, ventral lamellae of gills 2–5 bifid and festooned (Figs 19–22); gills of segment 2 opercular (Fig. 1). Paired posteromedial tubercles present on abdominal terga 1–9 (Figs 1, 2). Three caudal filaments present.

Adult.—Forewings with 2–3 detached marginal intercalaries between apex of main veins (Fig. 7) (Demoulin 1955).

Egg.—Single polar cap ringed by flap-like attachment structures (Figs 32–34).

***Melanemerella* Ulmer**
Figs 1–35

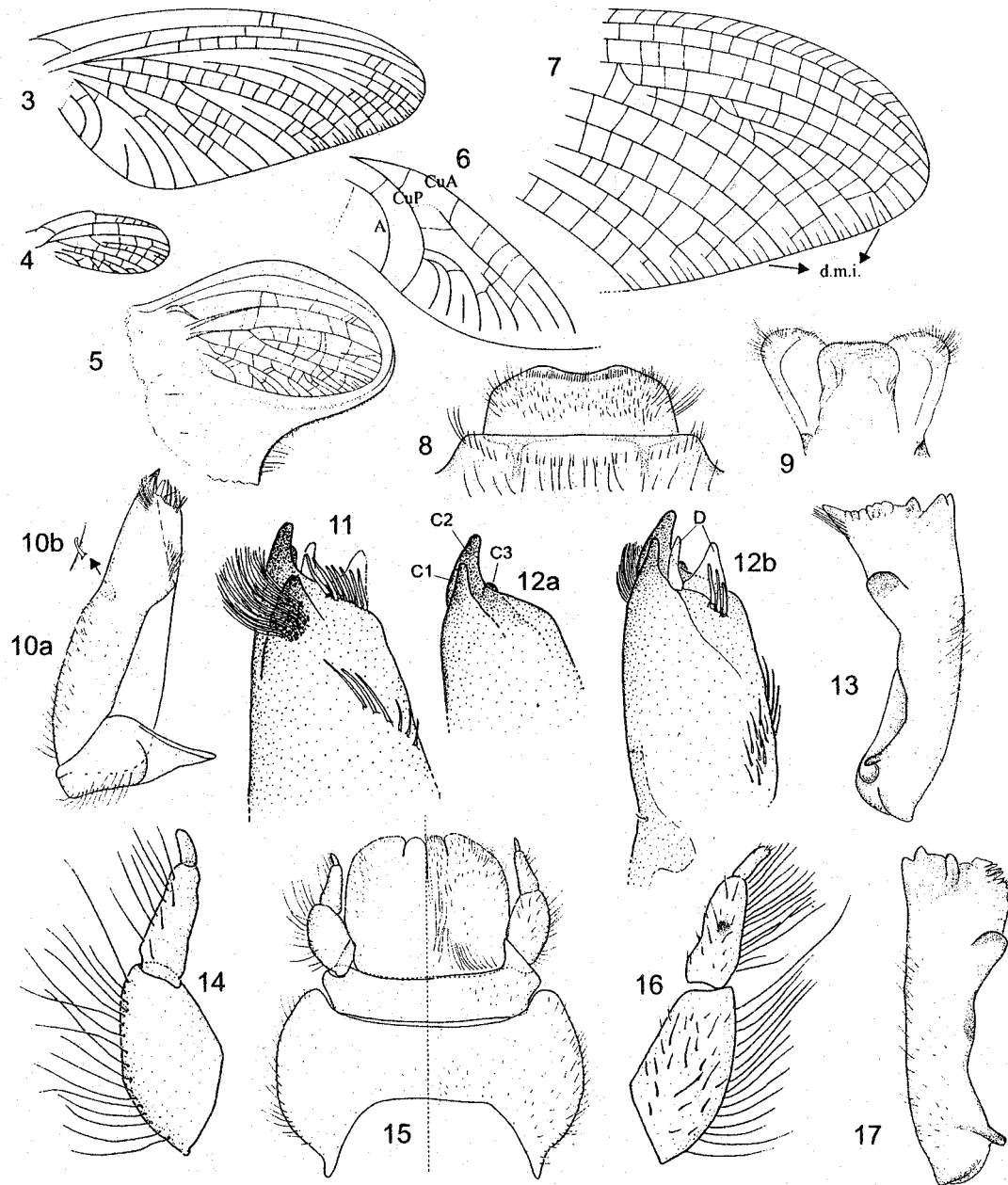
Type species: *Melanemerella brasiliiana* Ulmer 1920.

Melanemerella Ulmer 1920:43. Lestage 1925:258,

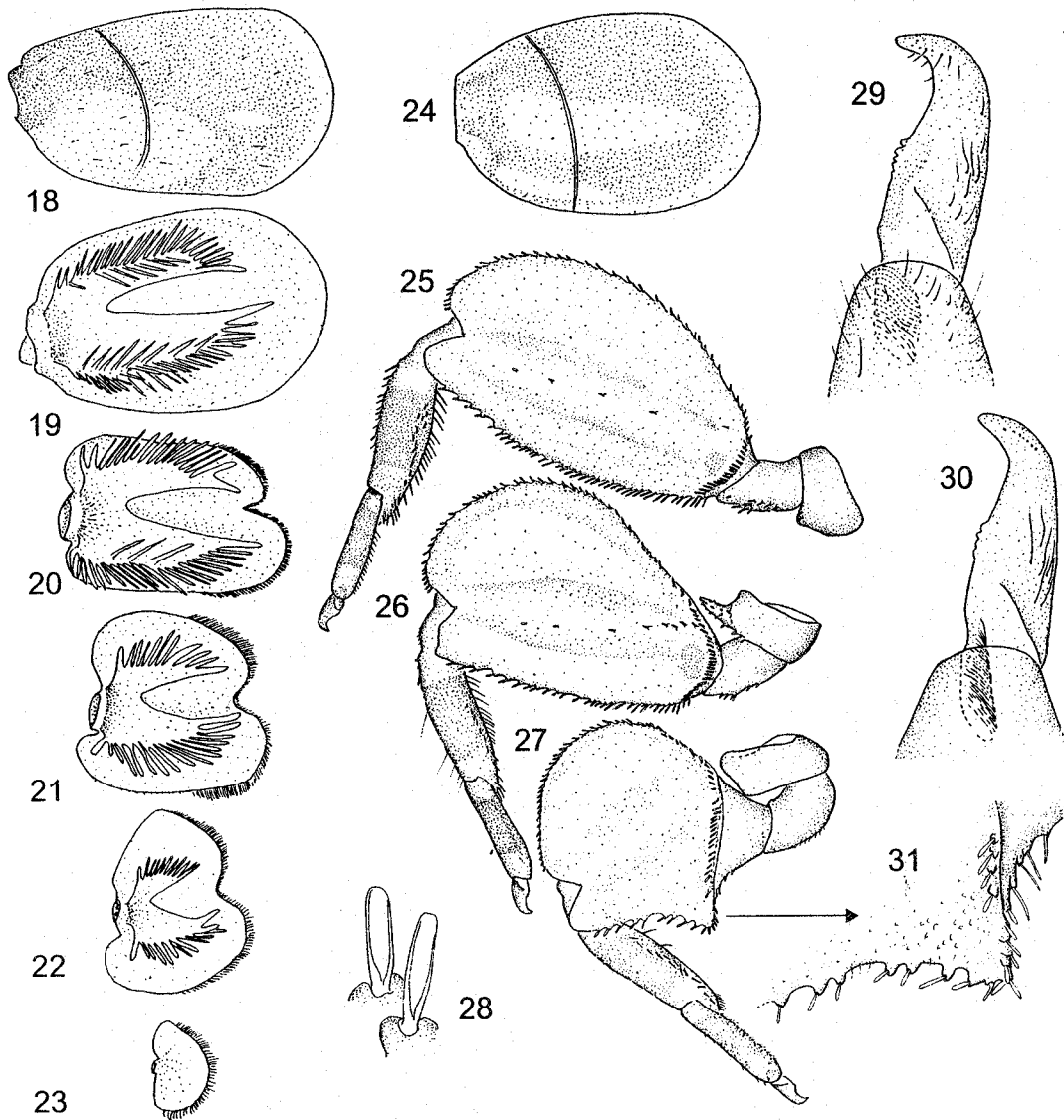
269, 271, 301. Demoulin 1955:214–216. Allen 1965:265. Wang and McCafferty 1996:99.

Description

Mature nymph (Figs 1, 2).—Head hypognathous, width 2 times length; anterior margin of frons shelf-like and fringed with setae; small genal projections present, posterolateral corners fringed with setae (Fig. 1). Occiput with median elevation. Eyes relatively small, located dorsally near posterolateral corners of head (Fig. 1). Eyes of male slightly larger than in female, not divided in upper and lower portion. Eyes separated on meson of head by distance twice width of eye in males, and by >3 times this length in females. Antennae $1/3$ longer than head; scape short, $2/3$ length of pedicel; flagellum long and thin composed of 24–26 annuli, basal annulus as long as pedicel, remaining annuli very short; flagellum 8 times length of scape and pedicel combined. **Mouthparts.** Clypeus reduced to narrow band. Labrum with shallow anterome-



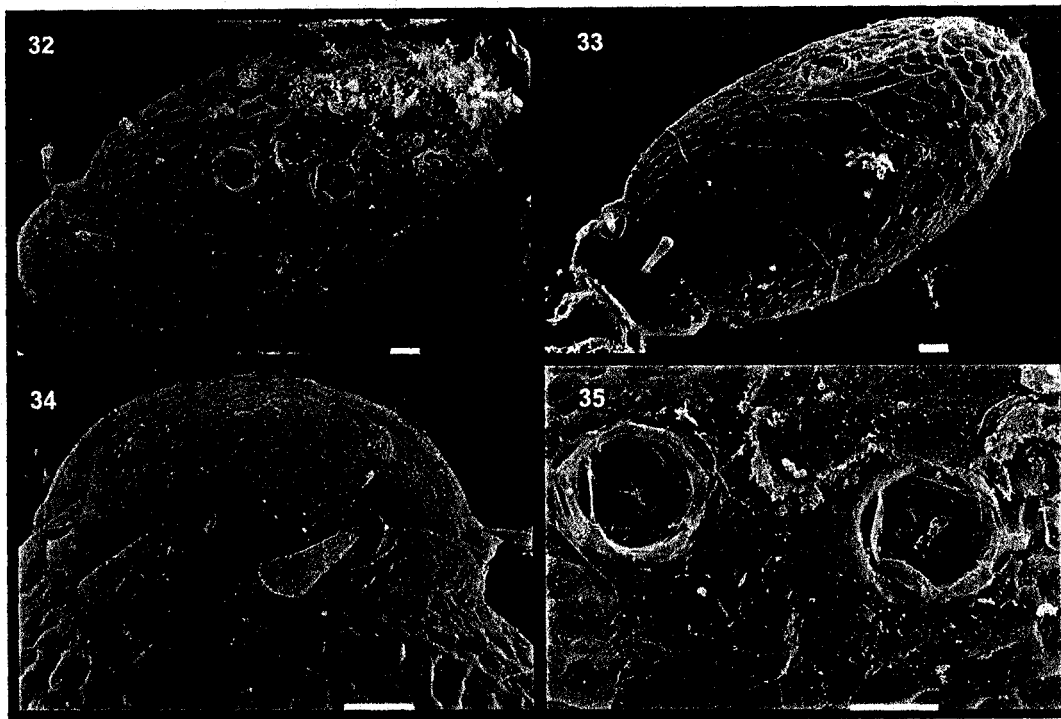
FIGS 3-17. *Melanemerella brasiliana*, wing venation and mouthparts: 3.—Forewing pad venation. 4.—Hind wing pad. 5.—Detail of hind wing pad. 6.—Detail of forewing pad (cubital [Cu] venation). 7.—Detail of apical third of forewing pad (d.m.i. = detached marginal intercalaries). 8.—Labrum, dorsal view (d.v.). 9.—Hypopharynx, ventral view (v.v.). 10a.—Right maxilla, v.v. 10b.—Maxillary palp, detail. 11.—Right maxilla, detail v.v. 12a.—Left maxilla, detail d.v. (setae omitted) (C1, C2, C3 = canines). 12b.—Left maxilla, detail d.v. (D = dentisetae). 13.—Right mandible, d.v. 14.—Right labial palp, detail d.v. 15.—Labium, d.v. at left, v.v. at right. 16.—Left labial palp, detail, v.v. 17.—Left mandible, d.v.



FIGS 18-31. *Melanemerella brasiliiana*, gills and legs: 18.—Gill 2, dorsal view (d.v.). 19-23.—Gills 2-6, ventral view. 24.—Gill 2, d.v. (color variation). 25.—Hind leg. 26.—Middle leg. 27.—Foreleg. 28.—Detail of spines on forefemora. 29.—Hind tarsal claw. 30.—Fore tarsal claw. 31.—Median projection of forefemora.

dian emargination (Fig. 8). Hypopharynx as in Fig. 9. Maxillae (Figs 10-12) with relatively stout cardo, palpi very small, setiform (Fig. 10b); 3 canines present (ventral one reduced, C3 in Fig. 12a); 2 parallel rows of setae near mediolateral corner, dorsal row with 2 large and 3 smaller setae (Fig. 12b), ventral one with 7-8 small setae (Fig. 11). Mandibles long and slender, with distal and proximal condyles widely separated (Figs 13, 17). Labium (Fig. 15) divided into 3

well-marked regions: submentum, mentum, and prementum; glossae and paraglossae partially fused; palpi 3-segmented, distal segment reduced (Figs 14, 16). Thorax. Pronotum almost as wide as head, with anterolateral corners sharply projected (Fig. 1), with concave lateral margins and pair of submedian small blunt tubercles near hind margin (Fig. 2). Mesonotum robust, distinctly wider than pronotum, with pair of submedian blunt elevations between



FIGS 32–35. *Melanemerella brasiliiana*, SEM photographs of eggs: 32–33.—General aspect. 34.—Detail of polar cap. 35.—Detail of micropyles.

Note good scan attached at end of document

wing pads and with median blunt hump on mesoscutellum. Forewing pads fused except on posterior $1/4$ – $1/6$ (Fig. 1). Metanotum and hind wing pads completely underneath forewing pads. Developing wings within wing pads (both pairs) with numerous detached marginal intercalaries and cross veins (Figs 3–7). **Legs.** (Figs 25–27). Femora discoidal, with short marginal spines and setae, spines inserted on elevated sockets; ratio length/width of forefemora = 1, middle femora = 0.73, and hind femora = 0.58; femora with mediolongitudinal ridge; forefemora with strong median projection on anterior margin (Figs 27–31); tibiae and tarsi short, combined length as long as femora; tibiae and tarsi with longitudinal row of spines on inner margin, on middle and hind tibiae, and additional row present on outer margin; tarsal claws relatively short and robust, with 4–5 small and blunt marginal denticles and double row of 4–5 setae near apex (Figs 29, 30). **Abdomen.** (Figs 1, 2). Segments 3–5 much shorter than the others, lateral zones of segments 3–6 concave (to accommodate gills). Gills present on abdominal

segments 2–6, those on segment 2 opercular and covering others completely; opercular gill ovoid to subrectangular, very sclerotized, with submedian weak transverse line (Figs 18, 24), ventrally with pair of membranous lamellae with fringed margins (Fig. 19). Gills 3–5 similar in form to gill 2, but with dorsal lamella membranous and notched apically (Figs 20–22); gill 6 formed by one small, semicircular lobe (Fig. 23). Abdominal terga with pair of submedian tubercles on hind margin, larger on segments 6–9 (Figs 1, 2). Posterolateral spines on segments 3–9, small on segments 3–5 and very large on 6–9 (Fig. 1). Male genitalia with a conspicuous, broad, and posteriorly projected styliger plate, penes apparently fused in single structure (forceps not distinguishable). Three caudal filaments present, subequal in length, $3/4$ length of body, with whorls of spines at apex of each annulation.

Egg.—Length, 175–180 μm ; maximum width, 85–88 μm . General shape (Figs 32, 33) ovoid, circular in cross section. One polar cap present, short and blunt (Fig. 34). Base of polar cap

TABLE 2. Data matrix of taxa and characters. Character coding as in Table 1. ? = missing character, - = not comparable, \$ = polymorphism (representing states 1 and 2).

Taxa	Characters						
	0	5	10	15	20	25	30
<i>Massartella</i>	00000101000001001000110-00000030						
<i>Neophemera</i>	01000100000002000000110-01100030						
<i>Austremerella</i>	0??0110000000??00000002?0020203?						
<i>Teloganella</i>	12001110000000010111?0?101112031						
<i>Manohyphella</i>	0??0110010000??0001100?01111???						
<i>Ephemereella</i>	010011000000010000100020--\$02031						
<i>Lithogloea</i>	01001100000001000010002001101030						
<i>Melanemerella</i>	1??0110000000??11121002011202031						
<i>Machadorythus</i>	0110121012---0000010011101200021						
<i>Ephemerythus</i>	11001210101010001010002101200001						
<i>Tricorythus</i>	1101121112---0001010002100200001						
<i>Tricorythopsis</i>	1211101112---0100020011111200022						
<i>Coryphorus</i>	11011-2112---0000020102101211011						
<i>Haplohyphes</i>	12011111101110101120011101200111						
<i>Leptoxyphodes</i>	0201101112---0101110011111210101						
<i>Tricorythodes</i>	1221101112---1001120011101200121						
<i>Leptoxyphes</i>	120111111111111001020011101200011						
<i>Yaurina</i>	12011011112121001020111101200011						
<i>Allenhyphes</i>	12011011112131001020111101200011						
<i>Traverhyphes</i>	12011011112121001020111101200011						

ringed by numerous flap-like attachment structures. Bases of these structures each arising from a circular area (Fig. 34). Chorionic surface sculptured with irregular netting of elevated ridges. At least 4 large and circular micropyles per egg (Fig. 35).

Melanemerella brasiliiana Ulmer

Melanemerella brasiliiana Ulmer 1920:44. Lestage 1925:301. Wang and McCafferty 1996:100.

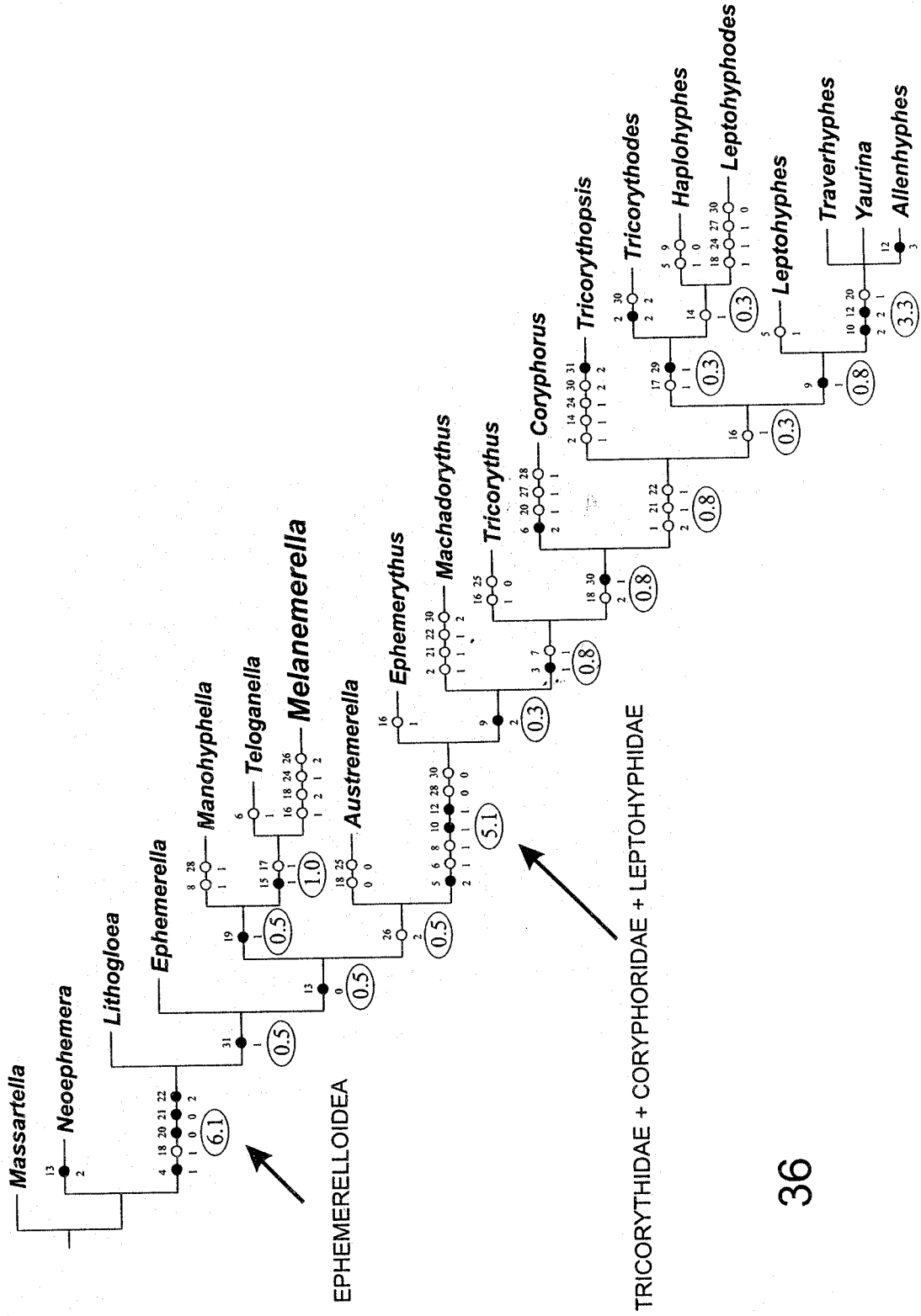
Description

Mature nymph.—Length: body, 9.2–13.2 mm; mesonotum and wing pads, 3.5–4.2 mm; caudal filaments, 8.0–9.5 mm; hind femora, 2.7–2.8 mm. General coloration brownish-gray. Head brownish-yellow tinged with dark brown on genae, median band between antennae and on pair of small circular marks located posteromedially to lateral ocelli, this pair of marks connected by transverse line, also brownish (Fig. 1). Antennae yellowish-translucent. Mouthparts yellowish-brown. Pro- and mesonotum dark brown with blackish marks, except lighter longitudinal median band (Fig. 1). Thoracic sterna grayish brown. Wing pads blackish. Legs yel-

lowish-brown with whitish and brownish marks; femora shaded with brownish-gray, with subcircular zones without pigmentation (Fig. 1); tibiae and tarsi with a wide median brownish band; legs lighter ventrally than dorsally, more marked on middle and hind legs. Abdomen yellowish-brown with brownish-gray elongated marks as in Fig. 1, posterolateral spines yellowish; tergum X yellowish-white, except hind and lateral margins, brownish-gray. Some nymphs with median lighter band of variable width along entire abdomen. Abdominal sterna grayish-brown. Intersegmental membranes grayish. Caudal filaments yellowish-brown, pale apically.

Male imago.—Unknown.

Biology.—The nymphs were collected in Campos do Jordão, a preserved area in São Paulo State. Along with this species, representatives of 24 other genera were also collected, belonging to 6 mayfly families. This richness of mayfly taxa is unusual in a neotropical stream. Gut contents contained mainly coarse particulate matter with little or no diatoms or sediment. Mouthpart characteristics suggest that the nymphs are primarily shredders: the mandibles (Figs 13, 17) are narrow, with the condyles



widely separated and the maxillary palpi are greatly reduced. Mature nymphs were collected in October and November, suggesting that the adults emerge in these months. No adults were found in the extensive light-trap collections from this locality deposited at the Museu de Zoologia, São Paulo.

Distribution.—Within the Ephemeroidea, the families Leptohiphidae and Coryphoridae are the only new world components. Their sister group, the family Tricorythidae, is widely distributed in Africa and Madagascar. Although species of Leptohiphidae are also found in North America, the group is considered mainly Neotropical. The recognition of *Melanemerella* as part of Ephemeroidea (and probably related to Teloganellidae) represents another record of a member of this group showing a vicariant distribution with other Gondwanian genera.

Remarks.—The nymph of *Melanemerella* can be distinguished from those of all other genera of Ephemeroidea by the following combination of characters: 1) lateral margins of submentum rounded (Fig. 15); 2) labial palpi 3-segmented, distal segment reduced (Figs 14–16); 3) maximum width of forefemur equals maximum length, and with an acute median projection on leading edge (Figs 27, 31); 4) middle coxae with a dorsal acute projection (Fig. 26); 5) gills present on segments 2–6, ventral lamellae of gills 2–5 bifid and festooned (Figs 19–22); 6) gills of segment 2 opercular (Fig. 1); 7) paired postero-medial projections present on abdominal terga (Figs 1, 2); 8) egg with a unique polar cap ringed by flap-like attachment structures (Figs 32–34); and 9) adult forewings with 3 marginal intercalaries between apex of main veins (Fig. 7).

Of the “ephemerellid” genera, only *Teloganella* from the Oriental region and *Melanemerella* present males with undivided eyes. Other characters shared by both genera are: 1) fore margin of head shelf-like and fringed with setae (Fig. 1); 2) femora of all legs disc-like (Figs 25–27); 3) prementum wider at base than at apex (Fig. 15); and in the adult 4) hind wing relatively small and with a notable and apically rounded costal projection.

Melanemerella differs from *Teloganella* in that abdominal gill 1 is absent (*Teloganella* has a small remnant) and the ventral lamellae are well developed and festooned with lobes (in *Teloganella*, the lamellae are reduced in size and not festooned, according to Wang et al. 1995, fig. 3). So far, these 2 genera seem to share more characters between them than with any other known ephemerelloid genera.

Material examined

BRAZIL: São Paulo: Parque Estadual Campos do Jordão, Córrego Galharada, 15.x.1998, Froehlich, Paprocki, 1 nymph; Córrego Galharada, 2.x.1986, Froehlich, Oliveira, 2 nymphs; no river data, 20.xi.1987, Froehlich et al., 2 nymphs; no river data, 18.xi.1987, Froehlich, Oliveira, 1 nymph; Córrego Galharada, 5.iii.1996, Froehlich, Holzenthal, Paprocki, 1 nymph.; Afluente Córrego Casquilho, 9.xi.1985, Froehlich, 1 nymph; Córrego Galharada, 10.xi.1985, Froehlich, 1 nymph. All the material is housed in the collection of the Museu de Zoologia, São Paulo, Brazil, except 3 nymphs deposited in Instituto-Fundación Miguel Lillo, Tucumán, Argentina.

Cladistic analysis

The character states observed in the studied taxa (Table 1) were scored in a matrix (Table 2). Some character states were not comparable in some of the taxa. For example, in the dipterous *Tricorythodes*, it was not possible to score the number of veins in the hind wings and, therefore, this character was scored as “-” in Table 2. In other cases with ≥ 1 unknown life stages, the missing information was scored as “?”. A character showing >1 state in a taxon was scored as a polymorphism, “\$”.

The matrix, analyzed with PIWE, resulted in a single, most parsimonious tree with a fit (Goloboff 1993b) of 228.7 (Fig. 36). This tree depicts the relations among the included taxa and the group support expresses the reliability of each grouping. A weak support means that the postulated relations could change easily with the addition of new characters.

←

FIG. 36. Single cladogram obtained from matrix (Table 2). Number above branch = character, number below branch = state, number in oval = Bremer support. Open circles = homoplasies, closed circles = apomorphies.

We conclude from this tree, and based on the Bremer support of the branches, that: 1) the only groups that are well supported (Bremer support above 5) are: (Tricorythidae (sensu Peters and Peters 1993) + (Coryphoridae + Leptohyphidae)); and Ephemerelloidea (see arrows in Fig. 36); 2) *Melanemerella* clearly belongs to the Ephemerelloidea; 3) *Melanemerella* belongs neither to the Leptohyphidae nor to the Tricorythidae or Leptophlebiidae; 4) the relationships among the families proposed by McCafferty and Wang (2000) for the members of Ephemerellidae (sensu Allen 1965) are very different from our results (compare our cladogram with their fig. 1); furthermore, the Bremer support for all of these branches is also very weak (below 1.0), implying that nodes could change or collapse with minimum alterations in the matrix; and 5) the position of *Melanemerella* is here restricted between 2 strongly supported nodes (arrows, Fig. 36), encompassing the *basal* Ephemerelloidea.

Discussion

Ulmer (1920) and Demoulin (1955) stated that the adult female of this species had a series of unique characters that did not allow them to assign it with certainty to any of the established families of Ephemerelloidea. The discovery of the nymph allowed us to describe the nymphal characters, emphasizing that gills are absent on abdominal segment 1. The new material also allowed us to observe a polar cap in the egg. The presence of gills on abdominal segment 1 and the absence of polar caps in the egg were used by Wang and McCafferty (1996) to justify the removal of *Melanemerella* from Ephemerelloidea. With the new information available, it became very clear to us that this genus belongs to the superfamily Ephemerelloidea, and more precisely to the group traditionally regarded as Ephemerellidae (sensu Allen 1965).

McCafferty and Wang (2000) proposed a new classification of the pannota mayflies, based on a phylogenetic study. Unfortunately, they did not recognize that *Melanemerella* was actually a member of this group, and did not include this taxon in their study. We could not include *Melanemerella* in McCafferty and Wang's (2000) analysis because they did not include a character matrix and did not state clearly which were their out groups.

A number of choices are possible: 1) assign *Melanemerella* to Ephemerellidae (sensu Allen 1965), as *incertae sedis* within this clearly paraphyletic group; 2) include it in one of the weakly supported families proposed by McCafferty and Wang (2000), probably Teloganellidae (a monobasic family); or 3) raise Melanemerellinae to family status (also monobasic). None of these choices is ideal. Placing *Melanemerella* in Teloganellidae probably would add more confusion to the already complicated relationships among the *basal* Ephemerelloidea, suggesting that the remaining families of the superfamily are monophyletic, which is unlikely. The relationships of the Ephemerellidae (sensu Allen 1965) remain uncertain in the present analysis. Thus, we prefer to raise *Melanemerella* to family Melanemerellidae, new status; to do otherwise would suggest a relationship not supported by the evidence.

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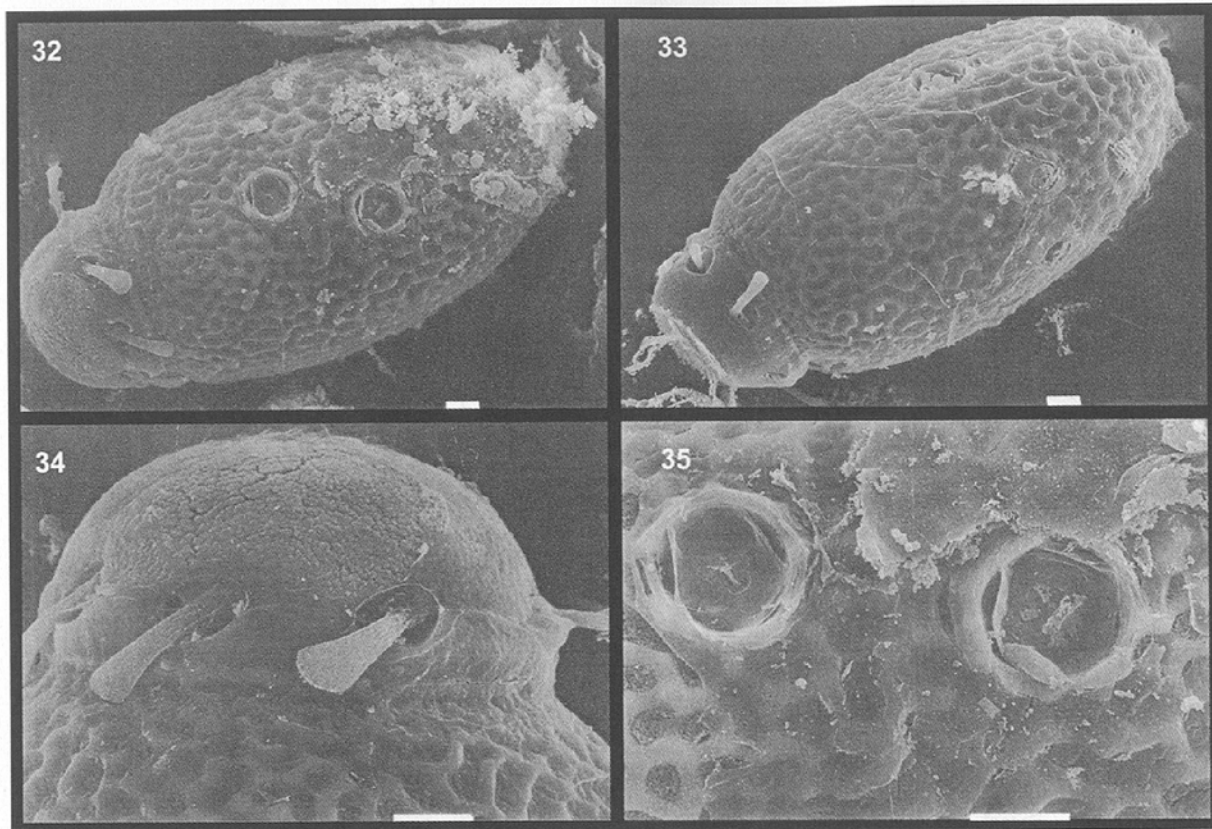
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FIGS 32-35. *Melanemerella brasiliiana*, SEM photographs of eggs: 32-33.—General aspect. 34.—Detail of polar cap. 35.—Detail of micropyles.